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Fish assemblages of shallow intertidal habitats of the Ria Formosa lagoon (South Portugal): influence of habitat and season

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ABSTRACT: Fish assemblages in seagrass and unvegetated habitats located in shallow intertidal creeks within the saltmarsh area of the Ria Formosa coastal lagoon were sampled with a Riley push net at 3 sites on a monthly basis over a 1 yr period. The objective was to test if both habitats support similar fish assemblages in terms of abundance, diversity, assemblage structure, and size distribution, and to investigate how site and season affect the assemblages. Fish assemblages associated with these habitats were significantly different in terms of diversity, abundance, and assemblage structure. Seagrass supported a larger number of species and greater diversity, while unvegetated habitat supported greater fish numbers but only of a few species. The habitats were dominated by different groups of resident species that were responsible for major differences in fish assemblage structure between habitats. *Pomatoschistus microps* and young-of-the-year (YOY) *Atherina presbyter* dominated the unvegetated habitat, while seagrass was dominated by a diverse group of species, in particular syngnathids and small labrids, revealing different habitat preferences. Site and season were determinant factors conditioning the role of habitat in structuring fish assemblages. Distance between habitats, site elevation, and the amount of marsh drained affected fish assemblages in both habitats. Seasonal fluctuations in the presence and abundance of YOY from marine migrant and resident species were responsible for comparable changes in fish assemblage structure in both habitats. Both habitats provide a distinctive nursery area for different species, while common species reveal ontogenic distributional changes between habitats, where smaller fish appear first in unvegetated creeks.

KEY WORDS: Fish fauna · Coastal lagoon · Saltmarsh · Intertidal habitats · Seasonal variations · Habitat association · Ria Formosa · South Portugal

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INTRODUCTION

Shallow intertidal habitats within saltmarsh areas can support important communities of fish species, especially the earlier life-history stages (juveniles), including those of many valuable commercial species (Weinstein 1979, Bozeman & Dean 1980, Kneib 1997). In many parts of the world, saltmarshes have been destroyed or considerably altered by human activities (Kneib 1997, Elliott et al. 2002). Therefore, a better understanding of the functioning of salt-

marshes is crucial for protecting these vulnerable habitats.

Most research on saltmarsh fish communities has been carried out in North America (Kneib 1997, Connolly 1999, Cattrijsse & Hampel 2006), with a more limited number of studies conducted in Australia (e.g. Morton et al. 1987, Connolly et al. 1997, Thomas & Connolly 2001) and South Africa (e.g. Paterson & Whitfield 1996, 2000a,b, 2003), and only very few carried out in Europe (e.g. Labourg et al. 1985, Cattrijsse et al. 1994). However, geographic characteris-

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tics of saltmarsh environments are extremely variable, in particular in terms of size, topography, and hydrology, which have relevant implications for fish use of intertidal marsh areas (Kneib 1997, Cattrijsse & Hampel 2006). U.S. Atlantic marshes are often located below mean high water, and therefore are inundated more frequently and for longer periods than European marshes, which are located mostly above mean high water, being inundated and accessible to fish only during spring high tides. These differences reveal the need for research on a range of saltmarsh types and geographical locations (Paterson & Whitfield 2003).

In order to assess the fish use of intertidal marsh habitats, several studies have investigated their fish communities, particularly in unvegetated creeks (Cain & Dean 1976, Shenker & Dean 1979, Bozeman & Dean 1980, Rountree & Able 1992, Paterson & Whitfield 1996, Paterson & Whitfield 2003), seagrass beds (Adams 1976, Pollard 1984, Smith et al. 1984, Bell & Pollard 1989), and vegetated habitats (e.g. Rozas & Minello 1998, Rozas & Zimmerman 2000). Other research compared the fish community present in different habitats, mostly between unvegetated creeks and subtidal seagrass (Weinstein & Brooks 1983, Heck et al. 1989, Ferrell & Bell 1991, Sogard & Able 1991, Connolly 1994, Paterson & Whitfield 2000a). In general, fish assemblages within intertidal marsh areas are formed mainly by estuarine resident and marine migrant species, with an important presence of juvenile fish, revealing that marshes may play a relevant role as nursery grounds. Comparative studies showed that fish communities associated with seagrass and unvegetated creeks within intertidal marsh areas were structurally different, with unvegetated habitats dominated by relatively few species.

In Europe most studies on intertidal marsh habitats concern unvegetated creeks and mud flats (Drake & Arias 1991a, Cattrijsse et al. 1994, Laffaille et al. 2000, Mathieson et al. 2000, Salgado et al. 2004a, Veiga et al. 2006), with no research on the differences between fish assemblages in intertidal seagrass beds and unvegetated creeks (Cattrijsse & Hampel 2006). In order to understand the role of these 2 shallow intertidal habitats in the overall ecology of the European saltmarshes, it is crucial to know if they are utilized by different ichthyofaunal communities. We tested the null hypotheses that: (1)

there are no differences between the 2 types of habitats with regard to diversity, abundance, assemblage structure, and size distributions; (2) there is no effect of marsh location; and (3) there are no seasonal changes in assemblage.

MATERIALS AND METHODS

Study area

This study was carried out in the western part of the Ria Formosa (Ria Faro-Olhão). The Ria Formosa is a large mesotidal coastal lagoon with a semi-diurnal tidal regime and an average spring tidal range of 3.1 m, extending for about 55 km along the Atlantic south coast of Portugal (36° 58' N, 8° 02' W to 37° 03' N, 7° 32' W), with a maximal width of 6 km (Fig. 1). Detailed descriptions of the characteristics of the Ria Formosa are given in Ribeiro et al. (2006, 2008).

Sampling design

Over a 1 yr period, from April 2001 to March 2002, fish fauna were collected from 3 seagrass (*Cymodocea nodosa*) pools and 3 nearby muddy-sandy bottom unvegetated pools, all located within intertidal creeks of the Ria Formosa marsh area (Fig. 1). The 6 locations are at 3 different marsh sites (A, B, and C), with each containing 1 seagrass and 1 unvegetated pool. Seagrass locations are generally deeper than unvegetated ones, with an average depth in seagrass of 0.70 to 0.80 m (maximum depth around 1 m, except in site A with 1.20 m) and around 0.50 m in unvegetated creeks (maximum depth around 0.70 m). Both habi-

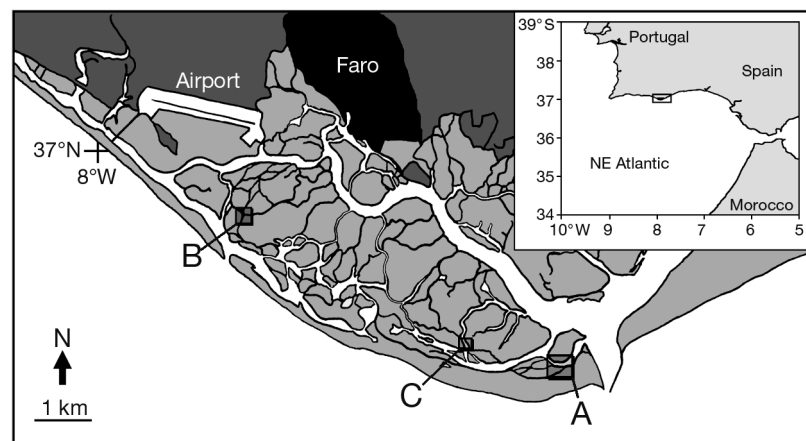


Fig. 1. Western part of the Ria Formosa lagoon (Ria Faro-Olhão) showing the location of the 3 sampling sites

tats at site A and the unvegetated habitat at site B are located approximately 1 m below high water spring tide level, while the seagrass habitat at site B and both habitats at site C are located right above the low water spring tide mark. In site C both habitats are contiguous and connected during the low tide; but in site A both habitats are connected but 20 m apart; while in site B the 2 habitats are not connected during low tide and are at a distance of 100 m. The creek at each site drained marsh areas with different sizes, with that at site B draining the largest area and that at site C the smallest area. Each habitat was sampled on a monthly basis using a Riley push net (Holme & McIntyre 1984) 1.5 m wide and 0.5 m high at the mouth, with a stretched mesh size of 2 mm in the cod end. At each of the 6 locations, sampling took place during low (spring) tides, in day time, and consisted in 3 replicate transects, 30 m long, covering an area of 45 m². In order to minimize differences in catch efficiency among samples each replicate took 1 min (0.5 m s⁻¹) (Eleftheriou & Holme 1984). In the laboratory, all fish were identified to species, counted, and measured to the nearest mm.

Data analysis

Shannon-Wiener diversity index (H') (Shannon & Wiener 1949) was calculated. Three factors were considered: site (A, B, and C); habitat (seagrass and unvegetated); and season (spring, summer, autumn, and winter). A 3-way factorial analysis of variance (ANOVA) was used to test for differences in the number of species, number of fish, and diversity indices, with all factors considered fixed (SAS Institute 1988). When significant main effects were detected in the multifactor ANOVAs, Tukey's honestly significant difference (HSD) test was used to find which means differed. Analysis was performed on the data with the level of significance set to $p \leq 0.01$ to minimize the chances of Type I errors occurring (Underwood 1997). Significant interactions between factors were examined graphically. Paired t -tests were used to compare average total length for the most important fish species present in both habitats.

Changes in composition and abundance of fish species (fish assemblage structure) were tested according to the same 3-factor design using the semi-parametric permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, 2005, McArdle & Anderson 2001). Analysis was conducted using the Bray-Curtis measure on $\log_{10}(x + 1)$ transformed data, and statistical significance was tested using 9999 permuta-

tions of residuals under a reduced model to obtain p -values (Anderson & ter Braak 2003). When significant at the 0.05 level, interaction terms were investigated through a posteriori pair-wise comparisons using 9999 random permutations to obtain p -values (Anderson 2005). To visualise significant effects obtained by the previous analysis, principal coordinate analysis (PCo) (unconstrained ordination) and canonical analysis of principal components analysis (constrained ordination) were used (CAP; Anderson & Robinson 2003, Anderson & Willis 2003, Anderson 2004). The relative contribution of species to the differences found was assessed using the correlation coefficient resulting between each species and the canonical axis in question, and the correlations of individual species ($|r| > 0.40$) with CAP axes 1 and 2 were plotted.

To compare the fish assemblage functional structure in relation to each factor, species were classified according to an ecological guild classification adapted from Elliott et al. (2007): catadromous (CA), marine stragglers (MS), marine migrants (MM), and lagoon resident (LR) species (adapted from estuarine resident). This classification was chosen because it is a logical extension of previous conceptual models, focusing on a revision and standardization of previous approaches. It also incorporates recent research on the life cycles of fishes in estuaries and takes into account the most recent management strategies for these valuable ecosystems.

RESULTS

Fish abundance and diversity

A total of 67 666 fish weighing 29 066 g were caught, representing at least 50 species and 17 families (Table 1). Average fish density at site A was 480.1 fish 100 m⁻² (37 species), 1498.6 fish 100 m⁻² (38 species) at site B, and 109.7 fish 100 m⁻² (32 species) at site C. The seagrass habitat accounted for 36 species and 5.9% of the fish (70.2 fish 100 m⁻²), while 41 species and 94.1% of the fish (1123.2 fish 100 m⁻²) were recorded in the unvegetated habitat. The overall number of species was higher in the unvegetated habitat, but within each site slightly more species were recorded in the seagrass habitat than in the unvegetated habitat (Table 1). Thirteen species were common to both habitats (8 LR and 5 MM), representing more than 96% and around 54% of the fish caught in the unvegetated habitat and seagrass, respectively. Ten species were present only in the seagrass and 14 only in unvegetated habitat (11 MS,

Table 1. Fish species caught over seagrass and unvegetated habitats, number of fish 100 m⁻² (N), relative abundance (Foc) and ecological classification (EG), size range (range TL), average total length (avg. TL), and t-test results comparing average total length for the most important fish species present in both habitats (t), ns: not significant. *p < 0.001

Species	EG	Seagrass						Unvegetated																									
		Site A		Site B		Site C		Site A		Site B		Site C		Range TL		Avg. TL (mm)																	
		N	N (%)	Foc	N	N (%)	Foc	N	N (%)	Foc	N	N (%)	Foc	N	N (%)		Foc	mm	mm														
<i>Anguilla anguilla</i>	CA	0.37	0.6	13.9	0.06	0.1	2.8	0.56	0.7	19.4	61.431	258.2	0.06	<0.1	2.8	—	—	218.0 *															
<i>Aphia minuta</i>	MS	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	30–40	34.2															
<i>Arnoglossus thori</i>	LR	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40	44.0															
<i>Atherina presbyter</i>	LR	4.14	6.3	47.2	2.28	2.3	27.8	1.60	2.0	11.1	10–93	47.9	29.08	3.2	52.8	109.63	5.0	88.9	42.10	33.3	36.1	10–81	22.3 *										
<i>Boops boops</i>	MM	—	—	—	0.06	0.1	2.8	—	—	—	35	36.0	—	—	—	—	—	—	—	—	—	—	—	—									
<i>Bothus podas</i>	MS	—	—	—	—	—	—	—	—	—	—	—	0.12	<0.1	2.8	—	—	—	—	—	—	—	—	—	35–40	39.0							
<i>Callionymus maculatus</i>	MS	—	—	—	—	—	—	—	—	—	—	—	0.25	<0.1	8.3	0.19	<0.1	8.3	—	—	—	—	—	—	—	30–55	42.9						
<i>Callionymus reticulatus</i>	MS	—	—	—	—	—	—	—	—	—	—	—	0.06	<0.1	2.8	—	—	—	—	—	—	—	—	—	—	40	42.0						
<i>Chelon labrosus</i>	MM	0.68	1.0	11.1	—	—	—	—	—	—	73–167	86.9	0.06	<0.1	2.8	6.60	0.3	36.1	—	—	—	—	—	—	—	15–118	37.3 *						
<i>Dentex maroccanus</i>	MS	—	—	—	—	—	—	—	—	—	—	—	0.06	<0.1	2.8	—	—	—	—	—	—	—	—	—	—	30	33.0						
<i>Dicentrarchus labrax</i>	MM	—	—	—	—	—	—	—	—	—	—	—	0.19	<0.1	2.8	13.52	0.5	27.8	—	—	—	—	—	—	—	15–145	45.8						
<i>Diplecogaster bimaculata</i>	LR	0.12	0.2	5.6	0.74	0.7	25.0	0.19	0.2	8.3	10–30	23.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	27.0 *					
<i>Diplodus annularis</i>	MM	0.37	0.6	5.6	0.56	0.6	19.4	0.68	0.8	22.2	12–109	53.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
<i>Diplodus bellottii</i>	MM	—	—	—	0.12	0.2	5.6	0.12	0.2	5.6	10–65	45.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
<i>Diplodus puntazzo</i>	MM	0.31	0.5	8.3	1.85	1.9	30.6	0.37	0.5	11.1	14–69	37.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—			
<i>Diplodus sargus</i>	MM	3.46	5.3	22.2	0.86	0.9	16.7	0.43	0.5	11.1	9–96	23.4	0.37	<0.1	11.1	1.91	<0.1	16.7	—	—	—	—	—	—	—	—	10–40	25.6 *					
<i>Diplodus vulgaris</i>	MM	4.94	7.5	30.6	5.49	5.5	25.0	5.12	6.4	36.1	10–75	33.8	4.26	0.5	19.4	3.21	0.1	19.4	—	—	—	—	—	—	—	—	15–50	22.3 *					
<i>Gobius couchi</i>	LR	0.25	0.4	5.6	0.62	0.6	25.0	0.06	0.1	2.8	29–79	58.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12–65	27.4 *					
<i>Gobius cruentatus</i>	MS	—	—	—	—	—	—	—	—	—	—	—	0.12	<0.1	5.6	0.06	<0.1	2.8	—	—	—	—	—	—	—	—	20–40	41.5 ns					
<i>Gobius niger</i>	LR	4.44	6.8	44.4	11.60	11.6	83.3	4.07	5.1	61.1	18–114	64.5	14.25	1.6	86.1	8.33	0.3	69.4	—	—	—	—	—	—	—	—	17–116	58.6 ns					
<i>Gobius paganelus</i>	LR	9.32	14.2	63.9	2.35	2.4	44.4	1.11	1.4	27.8	44–88	63.1	0.80	0.1	19.4	0.74	<0.1	19.4	—	—	—	—	—	—	—	—	40–110	60.8					
<i>Hippocampus guttulatus</i>	LR	—	—	—	0.19	0.2	5.6	0.74	0.9	13.9	103–137	11.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8.3	125–136	132.0 ns				
<i>Hippoc. hippocampus</i>	LR	—	—	—	—	—	—	—	—	—	—	—	0.06	<0.1	2.8	0.37	<0.1	2.8	—	—	—	—	—	—	—	—	8.3	65–105	84.0				
<i>Labrus viridis</i>	MS	—	—	—	—	—	—	—	—	—	—	—	0.06	<0.1	2.8	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
<i>Liza aurata</i>	MS	0.25	0.4	8.3	11.67	11.7	5.6	—	—	—	50–105	72.9	0.06	<0.1	2.8	169.51	2.9	44.4	—	—	—	—	—	—	—	—	14–124	33.2 ns					
<i>Monochinus hispidus</i>	MS	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—			
<i>Mullus surmuletus</i>	MM	—	—	—	0.06	0.1	2.8	—	—	—	40	41.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—			
<i>Nerophis lumbriciformes</i>	MS	—	—	—	0.12	0.1	5.6	0.06	0.1	2.8	145–150	148.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Nerophis ophidion</i>	LR	1.30	2.0	25.0	14.32	14.4	91.7	8.02	10.0	63.9	90–216	143.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Pagellus bogaraveo</i>	MM	0.37	0.6	11.1	0.25	0.2	11.1	0.06	0.1	2.8	20–115	6.71	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Parablennius gattorugine</i>	LR	0.06	0.1	2.8	—	—	—	—	—	—	55	54.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Parablennius pilicornis</i>	LR	—	—	—	0.06	0.1	2.8	—	—	—	50	55.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Parabl. sanguinolentus</i>	MS	—	—	—	0.06	0.1	2.8	—	—	—	50	55.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pomatoschistus microps</i>	LR	7.90	12.1	41.7	0.93	0.9	22.2	6.42	8.0	36.1	50–45	28.3	838.02	93.6	100	2663.77	91.9	100	—	—	—	—	—	—	—	—	—	50–45	28.3				
<i>Pomatoschistus minutus</i>	LR	0.06	0.1	2.8	—	—	—	—	—	—	25–35	29.2	1.05	0.1	2.8	—	—	—	—	—	—	—	—	—	—	—	—	25–35	29.2				
<i>Pomatoschistus pictus</i>	LR	0.49	0.8	11.1	0.68	0.7	11.1	0.25	0.3	5.6	15–35	24.9	3.58	0.4	47.2	0.74	<0.1	13.9	—	—	—	—	—	—	—	—	15–35	24.9					
<i>Salaria pavo</i>	LR	—	—	—	—	—	—	—	—	—	100	104.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	100	104.0					
<i>Sardina pilchardus</i>	MM	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Sarpa salpa</i>	MM	0.12	0.2	2.8	—	—	—	—	—	—	50–55	52.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Scorpaena notata</i>	MM	0.06	0.1	2.8	—	—	—	—	—	—	55–95	73.3	0.12	<0.1	2.8	—	—	—	—	—	—	—	—	—	—	—	—	55–95	73.3				
<i>Scorpaena porcus</i>	MM	0.68	1.0	25.0	1.30	1.3	30.6	0.49	0.6	22.2	40–160	88.9	0.74	0.1	25.0	0.62	<0.1	16.7	—	—	—	—	—	—	—	—	40–160	88.9					
<i>Serranus hepatus</i>	MS	—	—	—	—	—	—	—	—	—	—	—	0.19	<0.1	8.3	—	—	—	—	—	—	—	—	—	—	—	20–45	31.3					
<i>Sparus aurata</i>	MM	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20–70	47.5					
<i>Spondyliosoma cantharus</i>	MM	1.11	1.7	19.4	0.80	0.8	16.7	13.09	16.3	47.2	10–80	48.7	0.31	<0.1	11.1	0.31	<0.1	2.8	—	—	—	—	—	—	—	—	10–80	48.7					
<i>Symphodus bailloni</i>	LR	3.02	4.6	44.4	3.02	3.0	58.3	5.99	7.4	50.0	15–140	66.7	0.80	0.1	22.2	0.56	<0.1	11.1	—	—	—	—	—	—	—	—	15–140	66.7					
<i>Symphodus cinereus</i>	LR	1.11	1.7	22.2	9.75	9.8	83.3	2.72	3.4	47.2	10–120	50.8	0.12	<0.1	2.8	0.12	<0.1	5.6	—	—	—	—	—	—	—	—	10–120	50.8					
<i>Symphodus roissali</i>	MM	0.06	0.1	2.8	0.68	0.7	19.4	0.43	0.5	16.7	15–75	40.4	0.06	<0.1	2.8	0.06	<0.1	2.8	—	—	—	—	—	—	—	—	15–75	40.4					
<i>Symphodus abaster</i>	LR	17.90	27.4	91.7	11.98	12.0	69.4	13.95	17.3	58.3	40–110	75.6	—	—																			

8 MM, and 3 LR), representing less than 1% of the catch in each habitat. Finally, 13 species were present in the 2 habitats but not at all sites, representing approximately 45% and 3% of the catch in each habitat.

The size range and the average size of fish caught in the 2 habitats showed both fish assemblages were almost exclusively formed by YOY. However, for the species relatively abundant in the 2 habitats, particularly for MM species, the average sizes were significantly higher in the unvegetated habitat.

The 3-way ANOVA showed that site, habitat and season, were responsible for significant differences in mean number of species (Table 2). Tukey's HSD tests revealed that site B had significantly higher mean numbers of species than site A, while seagrass habitats had significantly higher mean numbers of species than unvegetated habitats, and mean number of species was significantly lower in winter than in the other seasons (Fig. 2).

All main effects were responsible for significant differences in mean number of fish, but site-habitat and habitat-season interactions were also significant, indicating that differences among and within each interacting factor should be assessed (Table 2, Fig. 3). For site-habitat interaction, unvegetated habitat had significantly more fish than seagrass within sites A and B, where the 2 habitats are separated by more than 50 m, but not for site C where habitat locations were almost contiguous (Fig. 3b). Within the seagrass habitat there was no significant site variation in fish abundance, while there were significant differences between all sites within the unvegetated habitat, with significantly more fish at site B, where the creek drains a much larger inter-

Table 2. *F* values and significance levels for the 3-way ANOVA of mean number of species, mean number of fish, and mean Shannon-Wiener index (*H'*), testing for differences between habitat, sites, and season

Effects	df	No. of species		No. of fish		Shannon-Wiener	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Habitat	1	71.51	<0.001	101.20	<0.001	362.99	<0.001
Site	2	5.74	0.006	46.53	<0.001	12.55	<0.001
Season	3	8.08	<0.001	5.56	0.002	1.90	0.143
Habitat × Site	2	0.22	0.803	44.85	<0.001	16.68	<0.001
Habitat × Season	3	0.51	0.676	5.32	0.003	5.94	0.002
Site × Season	6	0.81	0.567	2.37	0.044	1.73	0.135
Habitat × Site × Season	6	3.09	0.012	2.49	0.035	1.05	0.407

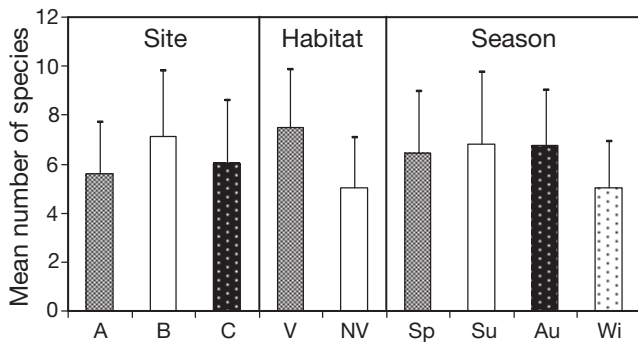


Fig. 2. Mean number of fish species for each factor level. Error bars represent +1 SE

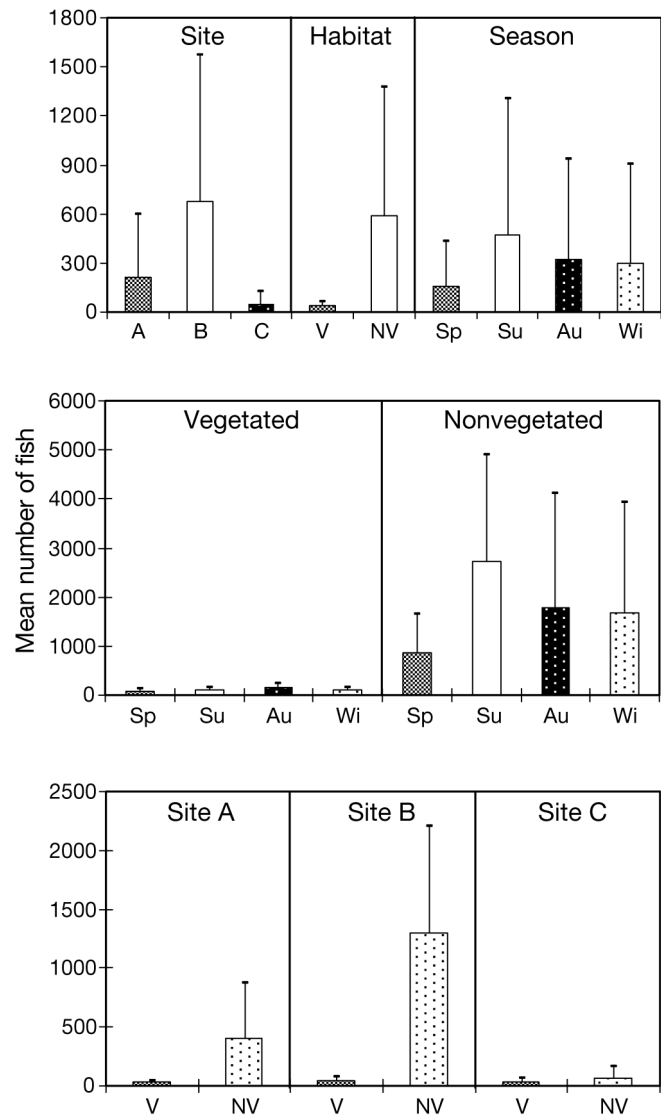


Fig. 3. Mean number of fish for each factor level and for all significant interactions between factor levels. Error bars represent +1 SE

tidal marsh area, than in sites A and C, and with more fish in site A than in site C, the creek drains the smallest intertidal marsh area of all 3 unvegetated locations (Fig. 3b). Considering habitat–season interaction, mean number of fish was always significantly higher in the unvegetated habitat than in seagrass independent of the season, and there were significant seasonal differences only for unvegetated habitat, which had more fish in summer than in winter and spring, but no significant differences between other pairs of seasons (Fig. 3c).

Overall, the Shannon-Wiener index was consistently higher in seagrass than in unvegetated locations, independent of site (Table 1). The 3-way ANOVA results for this index showed a significant habitat and site effect (Table 2, Fig. 4), but the site–habitat interaction was also responsible for significant differences (Table 2). The unvegetated location at site C (located near the subtidal edge) showed significantly higher diversity values than unvegetated locations at sites A and B (located in a more elevated position, further away from subtidal edge), while seagrass showed similar values within sites that were all significantly higher than those observed for unvegetated habitat at all sites (Fig. 4). These results reveal that the habitat effect was significant independent of the site effect, and that unvegetated habitats located at a less elevated position on the marsh, further away

from subtidal areas, had higher fish diversity. The habitat–season interaction was also significant, with no significant seasonal differences within seagrass habitat, but for the unvegetated habitat, summer values were significantly lower than in autumn and winter, and seagrass always had higher values than unvegetated habitat, independent of season.

Species composition

Unvegetated habitat locations within sites A and B were clearly dominated year round by the Gobiidae species *Pomatoschistus microps*, present in all samples and representing more than 90% of the total catch at each location (Tables 1 & 3). At site C, this species was again the most abundant and frequent but shared the dominance with the less common *Atherina presbyter*, which became dominant only in the autumn (68.1%). This latter species was also the second most abundant in unvegetated habitats at sites A and B, but with a lower relative importance. *A. presbyter* was represented mainly by young-of-the-year (YOY), with approximately 94% of the fish caught measuring less than 30 mm. Seasonally, *P. microps* clearly attained its greatest abundance in the summer, becoming less abundant in the remaining seasons, while *A. presbyter* was clearly less abundant in the winter (Table 3). *Gobius niger* was also an important species in terms of abundance and frequency of occurrence in unvegetated habitats, with similar numbers of fish at the 3 sites. These 3 resident species were present in the 3 unvegetated sampling locations all year round. *Chelon labrosus*, *Dicentrarchus labrax*, and *Liza aurata*, all represented exclusively by YOY, were relatively abundant only at site B, with the first two present most of all during the spring and summer, and the latter almost absent during the summer and more abundant during the autumn. *Diplodus vulgaris* was also fairly well represented in all unvegetated sites with relatively similar abundance levels, but only between February and July, where all fish caught were YOY. *Syngnathus abaster* and *S. typhle* were relatively abundant only in site C, during the autumn and winter. The higher values of relative importance for secondary species in site C were mostly due to the lower abundance of *P. microps* when compared with the other unvegetated locations.

In seagrass habitat locations within sites there was no clear species dominance, and, although the abundance of the most important species was variable from site to site, a group of 9 species represented

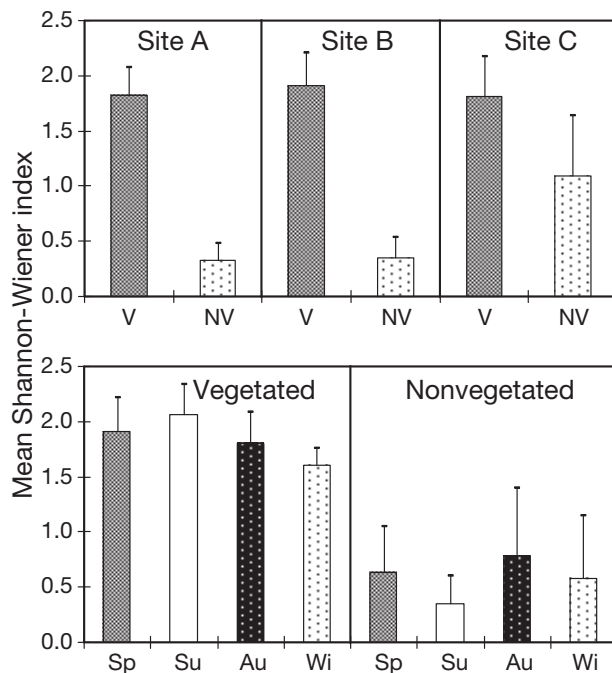


Fig. 4. Mean Shannon-Wiener index (H) for each factor level and for all significant interactions between factors levels. Error bars represent +1 SE

Table 3. Seasonal densities for the 20 most abundant fish species, in each habitat and at each sampling site and season

Species	Seagrass												Unvegetated												
	Site A				Site B				Site C				Site A			Site B			Site C						
	Spri.	Sum.	Aut.	Wint.	Spri.	Sum.	Aut.	Wint.	Spri.	Sum.	Aut.	Wint.	Spri.	Sum.	Aut.	Wint.	Spri.	Sum.	Aut.	Wint.					
<i>Atherina presbyter</i>	2.96	5.68	7.41	0.49	2.72	5.68	0.49	0.25	0.49	-	0.49	5.43	2.47	84.69	27.65	1.48	40.99	201.73	168.40	27.41	1.98	5.93	160.25	0.25	
<i>Chelon labrosus</i>	-	-	0.25	2.47	-	-	-	-	-	-	-	-	-	-	-	0.74	22.72	3.46	0.25	-	-	-	-	-	-
<i>Dicentrarchus labrax</i>	1.48	-	-	-	0.74	0.49	0.99	-	0.49	1.23	0.74	0.25	-	-	-	-	-	12.84	40.99	-	0.25	-	-	-	-
<i>Diplodus annularis</i>	0.99	-	-	0.25	1.98	-	0.99	4.44	0.49	-	0.25	0.74	-	-	-	-	-	-	-	-	-	-	-	0.49	-
<i>Diplodus puntazzo</i>	12.35	0.99	0.49	-	0.25	3.21	-	-	1.48	1.85	0.25	0.74	0.99	0.49	-	-	7.16	0.49	-	-	-	2.47	-	-	1.48
<i>Diplodus sargus</i>	19.26	0.49	-	-	15.06	0.74	-	3.70	8.64	11.85	0.25	0.74	16.79	0.25	-	-	2.22	9.63	-	0.99	12.35	-	-	-	-
<i>Diplodus vulgaris</i>	9.14	0.74	4.94	2.96	16.05	16.79	9.63	3.95	9.88	2.72	0.99	2.72	15.31	7.90	15.06	18.77	7.41	16.79	7.65	1.48	11.85	7.65	6.17	4.69	
<i>Gobius niger</i>	-	1.48	20.74	15.06	-	4.69	3.95	0.74	0.74	0.49	2.96	0.25	-	0.99	1.98	0.25	-	1.98	0.99	-	-	0.25	0.74	-	-
<i>Gobius paganellus</i>	-	0.49	0.49	-	-	46.67	-	-	-	0.49	-	-	-	0.25	0.25	-	37.04	12.84	233.83	55.06	-	-	0.25	0.74	-
<i>Liza aurata</i>	0.99	-	0.49	3.70	20.00	11.60	14.32	11.36	1.98	3.46	11.85	13.82	-	-	-	-	-	-	-	-	0.25	-	2.22	0.99	
<i>Nerophis ophidion</i>	2.47	0.74	2.72	25.68	0.25	0.74	1.23	1.48	0.99	1.98	9.63	13.07	546.67	1882.96	458.53	463.95	1126.17	3588.40	2817.78	3122.72	50.86	179.01	17.04	13.83	
<i>Pomatoschistus microps</i>	-	-	1.23	0.74	-	1.23	1.23	0.25	-	0.74	0.25	-	0.49	1.48	0.99	3.70	-	0.25	1.98	0.74	-	0.49	2.72	0.25	-
<i>Pomatoschistus pictus</i>	0.25	0.99	1.23	0.25	0.99	3.70	0.49	-	0.25	1.48	0.25	-	0.49	1.48	0.99	-	1.23	1.98	0.49	-	0.49	0.25	0.25	-	-
<i>Scorpaena porcus</i>	2.72	1.73	-	-	0.25	2.96	-	-	1.23	45.19	5.93	-	0.74	0.49	-	-	1.23	1.73	0.49	-	3.46	0.74	0.25	-	-
<i>Spondyliosoma cantharus</i>	1.98	5.93	2.96	1.23	1.98	6.17	3.46	0.49	0.49	16.54	6.42	0.49	0.74	0.49	-	-	1.23	1.23	0.25	-	0.49	0.74	0.25	-	-
<i>Symphodus bailloni</i>	2.47	-	1.73	0.25	2.96	13.09	20.74	2.22	3.45	3.46	3.95	-	0.49	-	-	-	-	-	-	-	0.49	0.74	2.96	-	-
<i>Symphodus cinereus</i>	9.63	13.58	18.77	29.63	3.95	0.49	8.89	34.57	0.25	2.47	40.25	12.84	-	-	-	-	0.25	-	-	-	1.48	0.25	8.40	5.43	-
<i>Syngnathus abaster</i>	0.25	-	1.98	0.74	0.74	0.25	0.74	0.25	0.49	0.74	1.73	0.49	-	0.25	0.25	-	1.23	0.25	0.25	-	-	0.49	-	-	-
<i>Syngnathus acus</i>	0.25	0.99	2.22	3.70	5.19	10.86	35.80	16.05	7.16	8.89	12.10	21.98	-	-	-	-	-	-	-	0.25	2.72	0.74	1.73	30.62	9.14
Total no. of fish	68.40	36.05	68.89	88.40	76.79	86.17	154.07	81.98	39.75	106.67	100.00	75.31	586.42	1987.65	516.30	489.14	1261.73	3881.23	3233.33	3213.58	86.42	197.78	235.31	36.30	

more than 70% of the catch in numbers at each seagrass location. Species of the Syngnathidae family were generally the most important, representing 38.6% of the catch in the seagrass, where the most important species were *Syngnathus abaster*, *S. typhle*, and *Nerophis ophidion*, which were more abundant in the autumn and winter. Sparidae, represented exclusively by YOY, was the second family in terms of relative importance with 20.7% of the catch, with *Diplodus sargus*, *D. vulgaris*, and *S. cantharus* the most important species, and particularly abundant in spring and/or summer but almost absent in the winter. The Gobiidae family was also important in terms of relative abundance, accounting for more than 10% of the catch in each seagrass sampling location. *Gobius niger*, *G. paganellus*, and *Pomatoschistus microps* were the most important Gobiidae species, with the first species less abundant in winter, while the last two were more important in autumn and winter. Finally, the Labridae family represented more than 6% of the catch in each seagrass location, with *Symphodus cinereus* and *Symphodus bailloni* the most important numerically and with higher abundances in the summer and autumn. In autumn, YOY of *Liza aurata* were particularly abundant in the seagrass habitat, but absent from site B except for November.

Fish assemblage structure

PERMANOVA results showed that there were significant differences in fish assemblage structure due to all 3 main effects, where habitat was the factor responsible for most of the variation within samples, with *F* values almost 8x higher than the other factors (Table 4). The unconstrained ordination plot using the first 2 principal coordinates axes show a clear sep-

Table 4. Results of PERMANOVA testing for differences in fish assemblage structure, in response to habitat, site, season, and interactions effects

Effects	df	MS	<i>F</i>	<i>p</i>
Habitat	1	50 905.25	79.35	0.0001
Site	2	6767.74	10.55	0.0001
Season	3	7618.02	11.87	0.0001
Habitat × Site	2	4405.44	6.87	0.0001
Habitat × Season	3	743.34	1.159	0.3080
Site × Season	6	1349.95	2.10	0.0003
Habitat × Site × Season	6	837.24	1.31	0.1197
Residual	48	641.54		
Total	71			

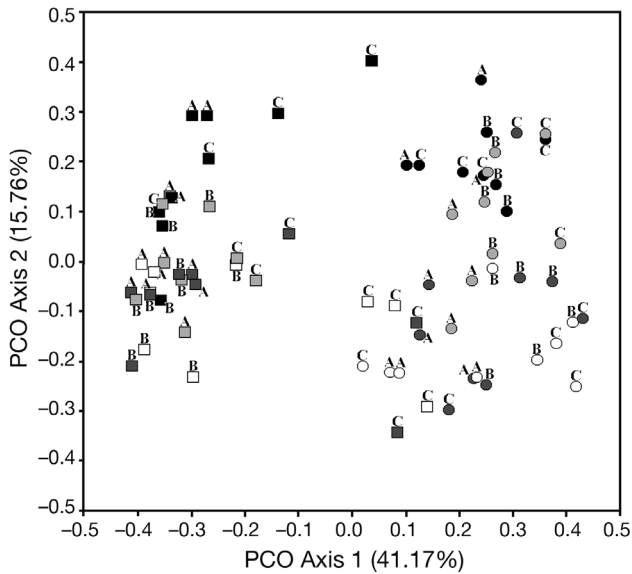


Fig. 5. Unconstrained ordination plot using principal coordinate analysis of the fish species abundance data representing each sample taken in both habitats, at 3 sites and during 12 mo. squares: unvegetated habitat; circles: seagrass; black: spring; light grey: summer; dark grey: autumn; white: winter; letters represent the 3 sites

Table 5. Results of pair-wise comparisons tests for terms for significant interactions found in the PERMANOVA analysis (habitat–site and site–season interactions). * $p < 0.001$; ** $p < 0.01$; *** $p < 0.05$; ns: not significant

Tests among levels of habitat within each level of site				
Habitats	Site A	Site B	Site C	
Seagrass–Unvegetated	4.5763*	5.7394*	3.1123*	
Tests among levels of site within each level of habitat				
Sites	Seagrass	Unvegetated		
A,B	2.2876 *	2.9555 *		
A–C	2.0597 **	2.1577 *		
B,C	1.2051 ns	3.1999 *		
Tests among levels of site within each level of season				
Sites	Spring	Summer	Autumn	Winter
A,B	1.1890 ns	1.2476 ns	1.3916 ns	4.5763 ns
A–C	1.2333 ns	1.5553 ns	1.3965 ns	4.5763 ns
B,C	1.3445 ns	1.5166 ns	1.1322 ns	4.5763 ns
Tests among levels of season within each level of site				
Seasons	Site A	Site B	Site C	
Spring–Summer	1.7562 ns	1.1718 ns	1.2163 ns	
Spring–Autumn	2.0423 ***	1.1546 ns	1.8242 **	
Spring–Winter	1.9026 ***	1.2893 ns	1.9695 **	
Summer–Autumn	1.0276 ns	1.9214 ns	1.0521 ns	
Summer–Winter	1.6742 ns	1.7714 ns	1.4453 ns	
Autumn–Winter	1.1296 ns	1.0671 ns	1.3826 ns	

aration of samples by habitat type along the 1st axis, which explained 41.17% of the variation within samples (Fig. 5). All seagrass samples are distributed on the right side of the plot, while samples collected in unvegetated locations are on left side, with the exception of all winter and 2 autumn samples taken at site C, which are mixed with seagrass samples collected in those seasons. However, habitat–site interaction was significant, with pair-wise comparisons showing significant differences in fish assemblage structure among the 2 habitats independent of site levels, and also revealing significant differences among all sites within each habitat, except between sites B and C within seagrass (Table 5). These results were perfectly evident in the canonical plot used to discriminate differences among terms of the significant habitat–site interaction (Fig. 6a). Season effect revealed significant differences between all seasons except between summer and autumn, but site–season interaction was also significant. Pair-wise comparisons showed no significant seasonal changes in fish assemblage structure among sites within each season level, but revealed significant differences between spring and both autumn and winter, within sites A and C, and significant differences between summer and winter only at site C, while significant differences between spring and summer were observed only for site A. No significant seasonal differences were observed within site B (Table 5). The canonical plot used to discriminate differences among terms of the significant site–season interaction shows a clear separation of spring samples from autumn and winter samples at sites A and C. Samples from summer and winter were only slightly separated for site C. Samples from site B were very disperse throughout the plot area, and no clear separation seasonal of samples is evident (Fig. 7a).

The correlation of individual species ($|r| > 0.40$) with CAP axes 1 and 2 regarding habitat–site interaction terms showed that *Diplodus annularis*, *Diplodus puntazzo*, *Nerophis ophidion*, *Syngnathus abaster*, *Symphodus bailloni*, *Symphodus cinereus*, and *Symphodus typhle* were highly correlated with seagrass samples, with *Syngnathus abaster* particularly correlated with seagrass samples at site A, and the remaining species particularly correlated with seagrass samples at sites B and C (Fig. 6a). On the other hand, *Pomatoschistus microps* was highly correlated with unvegetated samples, in particular at sites A and B, and *Atherina presbyter*, *Chelon labrosus*, *Dicentrarchus labrax*, and *Liza aurata* were only highly

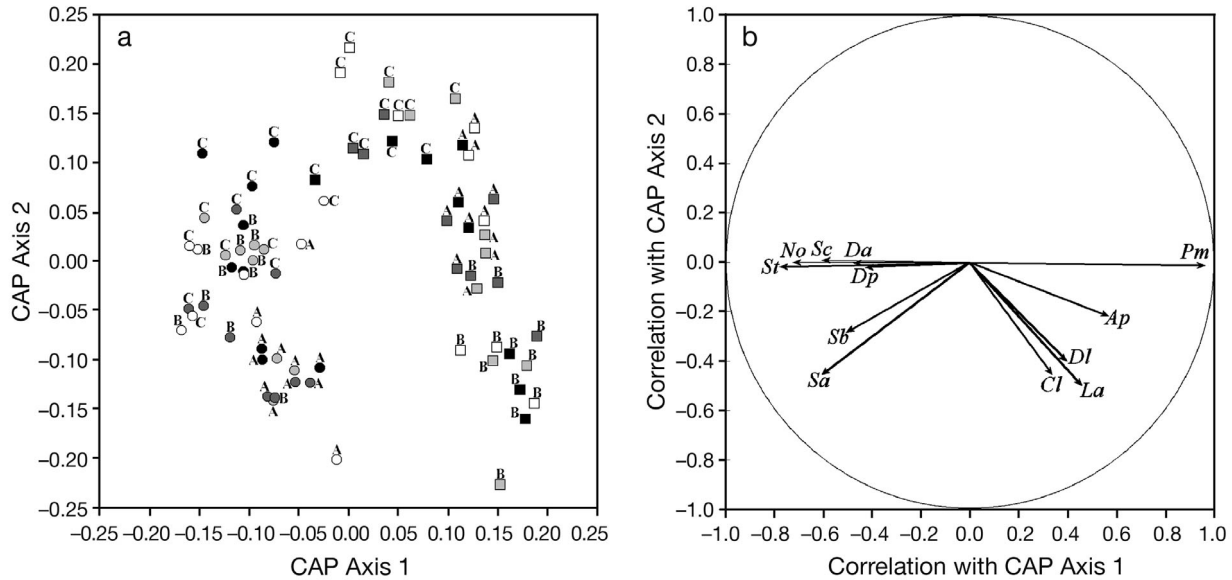


Fig. 6. (a) Constrained ordination plot using CAP analysis of the fish species abundance data, in order to discriminate differences among terms of the significant habitat–site interaction (see Fig. 5 for further explanations). (b) Correlations ($|r| > 0.40$) of fish species with the 2 previous CAP axes. *Ap*: *Atherina presbyter*; *Dl*: *Dicentrarchus labrax*; *Cl*: *Chelon labrosus*; *Da*: *Diplodus annularis*; *Dp*: *Diplodus puntazzo*; *La*: *Liza aurata*; *No*: *Nerophis ophidian*; *Pm*: *Pomatoschistus microps*; *Sa*: *Syngnathus abaster*; *Sb*: *Symphodus bailloni*; *Sc*: *Symphodus cinereus*; *St*: *Syngnathus typhle*

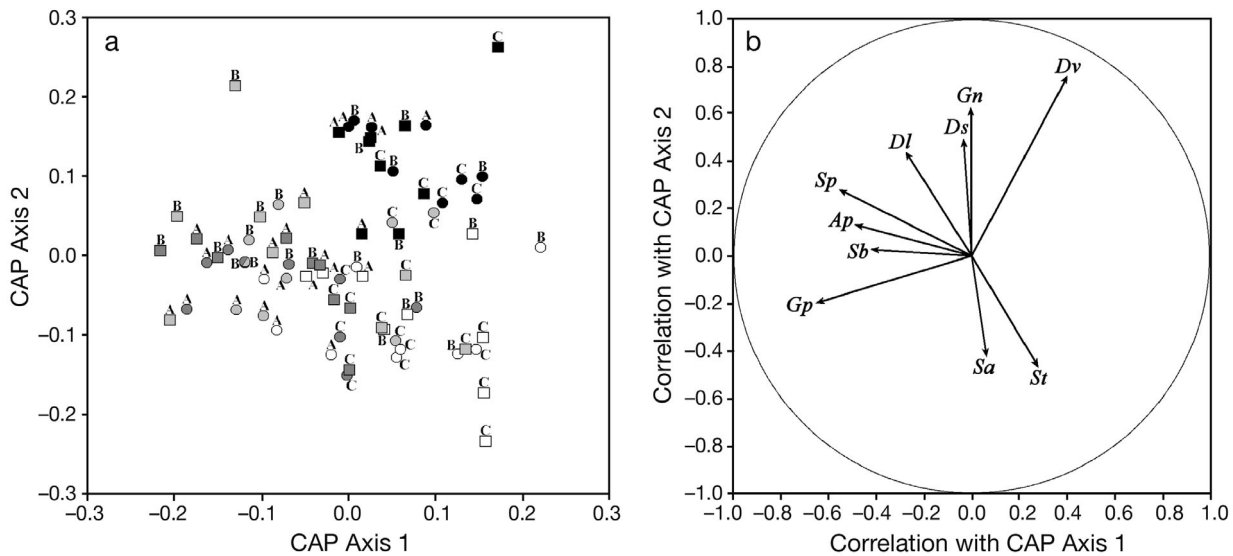


Fig. 7. (a) Constrained ordination plot using CAP analysis of the fish species abundance data, in order to discriminate differences among terms of the significant site–season interaction (see Fig. 5 for further explanations). (b) Correlations ($|r| > 0.40$) of fish species with the 2 previous CAP axes

correlated with unvegetated samples from site B (Fig. 7b). Considering site–season interaction terms, the correlation of individual species ($|r| > 0.40$) with CAP axes 1 and 2 revealed that *Diplodus vulgaris* was highly correlated with spring samples, while *Gobius niger* and *Diplodus sargus* were correlated to spring samples mostly at sites A and B. *Syngnathus abaster*

and *Syngnathus typhle* were highly correlated with autumn and winter samples, in particular at site C. *Symphodus bailloni* and *A. presbyter* were correlated with summer and autumn at sites A and B and *Gobius paganellus* was well correlated only at site A. *Scorpaena porcus* and *Dicentrarchus labrax* were well correlated to summer samples at site B.

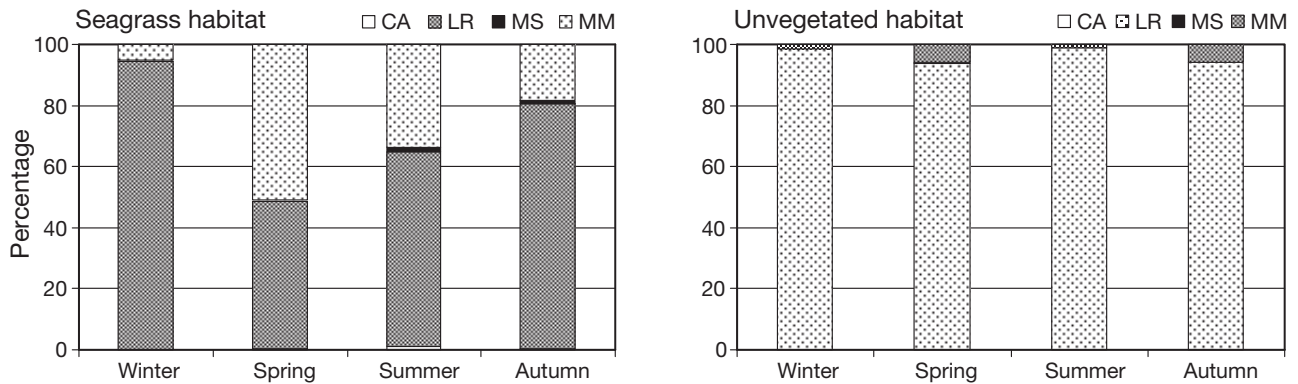


Fig. 8. Percentage of fish number by ecological guild caught in each season over seagrass and unvegetated habitats. CA: catadromous; LR: lagoon residents; MS: marine stragglers; MM: marine migrants

The resident species were always the most important ecological guild present in each sample location, both in terms of number of species and fish abundance (Table 1). This was particularly evident for fish abundance in the unvegetated habitat, where resident species represented more than 95% of fish caught. MM was the second most abundant group, with 26.5% in seagrass, but representing only 3.2% in unvegetated habitat. MS was the least abundant group in both habitats. The 2 habitats showed similar seasonal patterns for ecological guilds in terms of fish abundance, characterized by an increase in relative importance of YOY from MM in the spring, followed by a progressive decrease in summer and autumn, reaching a minimum during the winter, when resident species became clearly dominant in both habitats (Fig. 8). This pattern was more evident in the seagrass habitat, where the MM became dominant in the spring, while in the unvegetated habitat the resident species were clearly dominant all year round.

DISCUSSION

Habitat differences

Fish assemblages associated with seagrass and unvegetated habitats, both located within the Ria Formosa intertidal marsh creeks, showed clear differences in terms of fish diversity, abundance, and assemblage structure. Fish diversity in these 2 intertidal habitats was higher over seagrass than in nearby unvegetated areas, as found in subtidal channels of the Ria Formosa (Ribeiro et al. 2006), and also as reported in other similar studies in NE coast of USA (e.g. Weinstein & Brooks 1983, Sogard & Able 1991), and in Australia (Ferrell & Bell 1991, Connolly 1994a), but in contrast to findings of Paterson & Whit-

field (2000a) who reported similar diversities between these 2 habitats in a South African estuary. These authors found similar total number of species in both habitats, very close to those found in the present study, but most of the species found in the unvegetated habitat of Ria Formosa were sporadic, resulting in an average number of species significantly higher in the seagrass. In spite of this, differences in diversity were most of all due to an overwhelming dominance of one single species, *Pomatoschistus microps*, in the unvegetated habitat, compared to the seagrass habitat where there was no dominance by a particular species, rather than to substantial differences in number of species observed in each habitat. Again, studies from the NE coast of the USA and Australia showed that intertidal unvegetated marsh creek habitats support high fish densities, but only from few species (e.g. Cain & Dean 1976, Kneib 1987), and in general higher than nearby seagrass (Weinstein & Brooks 1983, Ferrell & Bell 1991, Sogard & Able 1991). In contrast, some studies from South African estuaries (Branch & Grindley 1979, Beckley 1983, Paterson & Whitfield 2000a) reported higher fish densities in seagrass than in unvegetated marsh creeks. Studies in European estuarine salt-marshes found, like in the present study, that *P. microps* was the most dominant fish species in the intertidal marsh areas, in particular in unvegetated marsh creeks (Drake & Arias 1991a,b, Cattrijsse et al. 1994, Hampel et al. 2003, Salgado et al. 2004a,b, Cattrijsse & Hampel 2006, Veiga et al. 2006). The huge abundance of *P. microps*, and to a lesser extent the abundant presence of *Atherina presbyter* YOY, were clearly responsible for the much greater fish densities in the unvegetated habitats, except for site C where differences in abundance between habitats were not significant. These abundances are related to the capacity of these species to distribute and

move along the tide edge, allowing them to use the intertidal marsh area during the high tide, and to withdraw during the ebb tide, returning to the very shallow intertidal creeks and pools where they remain concentrated during the low tide (Cattrijsse et al. 1994, Kneib 1997). The use of the intertidal marsh surface allows them to find shelter, avoid predation, and feed in the productive intertidal saltmarsh foraging grounds that are only available for short periods twice a day during the high tide in the European saltmarshes (Hampel & Cattrijsse 2004).

Although the abundant presence of Atherinidae species (e.g. *Atherina boyeri* and *A. presbyter*) in south European estuaries and coastal areas (Atlantic and Mediterranean) is well known (Labourg et al. 1985, Bouchereau et al. 2000, Guidetti & Bessotti 2000), the abundant presence of YOY from Atherinidae family in intertidal areas of European saltmarshes is not well documented. However, in shallow littoral zones along the U.S. coast, species of the Atherinidae family (e.g. *Menidia menidia*) use the tidal edge in order to gain access to intertidal marsh habitats (Allen 1982, Rountree & Able 1992), and in particular their larvae and juveniles use these habitats during the first period of their life history (Middaugh 1981, Middaugh & Takita 1983, Conover & Kynard 1984). The dynamic pattern of distribution along the tide edge could explain why *Pomatoschistus microps* and *A. presbyter* YOY were so much more abundant at low tide in the unvegetated creek than in seagrass, since the unvegetated habitats locations were less deep, and therefore closer to the tidal edge.

Intertidal marsh habitats ichthyofaunal assemblages were characterized by the presence of MM and LR, with LR dominating both assemblages, as reported in several studies (Rakocinski et al. 1992, Kneib & Wagner 1994, Thomas & Connolly 2001), but in contrast to Paterson & Whitfield (2000a) who reported the dominance of MM in unvegetated creek marsh habitats. However, fish assemblage structure associated with shallow intertidal seagrass differed from those found over unvegetated habitats, as reported in similar comparative studies (Weinstein & Brooks 1983, Heck et al. 1989, Ferrell & Bell 1991, Sogard & Able 1991, Connolly 1994, Paterson & Whitfield 2000a). Distinct fish assemblage structure was mostly due to differences in abundance of common species among habitats as found in the NE coast of the United States (Weinstein & Brooks 1983, Sogard & Able 1991), rather than species specifically present in one habitat, as found in a South African estuary (Paterson & Whitfield 2000a) and in the SW

coast of Australia (Ferrell & Bell 1991, Connolly 1994). Nevertheless, the most abundant species in each habitat were LR species predominantly represented in one single habitat, reflecting a clear habitat preference. *Pomatoschistus microps* and YOY of *Atherina presbyter* were by far the predominant species in the unvegetated habitat, while the syngnathids *Nerophis ophidion*, *Syngnathus abaster*, *Syngnathus typhle*, and small labrids *Symphodus bailoni* and *Symphodus cinereus* were predominant in the seagrass, and poorly represented in unvegetated habitats (except in site C, during autumn and winter). The close association of syngnathids, in particular the *Syngnathus* genera, to seagrass habitats in coastal and estuarine environments is well known in Atlantic-Mediterranean and Indo-Pacific regions, where they are among the most frequent and abundant species in these habitats (Pollard 1984, Howard & Koehn 1985, Rossi 1986, Franzoi et al. 1989). Differences in fish assemblage structure, associated with habitat preferences from LR species, reveal their importance as a structuring component of the fish assemblage in the intertidal marsh habitats in the Ria Formosa, and also indicate their potential importance in the functioning of the marsh ecosystem as a vector in the transfer of intertidal production to subtidal areas (Kneib & Wagner 1994, Kneib 1997). Although some YOY from MM species did not show any clear habitat preference, in particular *Diplodus vulgaris* and *Diplodus sargus*, others showed preference for seagrass habitats, such as *Diplodus annularis*, *Diplodus puntazzo*, and *Spondyliosoma cantharus*, while others such as *Chelon labrosus*, *Dicentrarchus labrax*, and *Liza aurata* preferred unvegetated habitats. These last 3 species were present almost exclusively in the unvegetated location at site B, probably because recruitment into the intertidal areas is likely a random process for most MM species, but their absence or lower abundance in the nearby seagrass habitat should indicate a habitat selection and preference. The presence of YOY of *Dicentrarchus labrax* and Mugilidae species (e.g. *C. labrosus* and *L. aurata*), as well as their foraging activities in the unvegetated intertidal marsh creeks has been reported in several west Atlantic European saltmarshes (Kelley 1988, Cattrijsse et al. 1994, Laffaille et al. 2000, 2002, Hampel et al. 2005, Veiga et al. 2006), and in Mediterranean coastal lagoons (Labourg et al. 1985, Bouchereau et al. 2000). The presence of mugilid YOY in intertidal creeks is also common in other parts of the world (Shenker & Dean 1979, Bozeman & Dean 1980, Paterson & Whitfield 2000b, Thomas & Connolly 2001).

Habitat preferences could be the result of differences in species dietary regimes (Burchmore et al. 1984), since the 2 habitats provide distinct and abundant food resources (Whitfield 1988), but also a consequence of different predatory avoidance strategies (Bell & Pollard 1989), where seagrass, a structurally more complex habitat (Orth et al. 1984), could provide an opportunity to employ cryptic mechanisms to blend into background structure (e.g. labrids and syngnathids), while the unvegetated environment is more suitable for schooling (e.g. *Atherina presbyter* and *Liza aurata*) or camouflage against the sediment (e.g. *Pomatoschistus microps*), as observed by Paterson & Whitfield (2000a). Diet studies of 0-group sea bass in the Tagus estuary (Cabral & Costa 2001) and the Po River delta (Ferrari & Chiericato 1981) have shown that smaller sized stages (<30 mm standard length) are predominantly planktophagous, while larger juveniles feed preferentially on macroplankton (Decapoda, Mysidacea, Isopoda, and fish larvae), that may be more abundant and easier to capture in the structurally less complex, unvegetated habitat. The preference of syngnathids and labrids in seagrass habitats in the Ria Formosa lagoon was also reported for subtidal areas within the main channels (Erzini et al. 2002, Ribeiro et al. 2006).

Site differences

Habitat has a major role in structuring the fish assemblages present in the Ria Formosa intertidal marsh creeks, but significant habitat–site interactions showed that site was a determinant factor conditioning the habitat role. Site characteristics such as site elevation, distance to the marsh, water depth, and submergence duration have a relevant effect on the fish assemblages present in the intertidal marsh area (Kneib & Wagner 1994, McIvor & Rozas 1996, Kneib 1997, Thomas & Connolly 2001). Differences in fish assemblages between habitats, although significant at all sites, were less evident at site C, where both habitats were located near the subtidal edge, and only a few m distant from each other. Several studies have shown that fish assemblages associated with different habitats located within subtidal areas tend to be more similar than those in intertidal areas, since subtidal areas are more accessible to all fish species (Kneib & Wagner 1994, Kneib 1997). On the other hand, Ferrell & Bell (1991) showed that differences in fish assemblages between unvegetated and seagrass habitats were negatively related to distance between habitats.

In seagrass, differences among sites were not significant in terms of fish diversity and abundance, but in terms of assemblage structure there were significant differences between sites B and C, both located near the subtidal edge, and site A, located in a more elevated intertidal position. These differences in the fish assemblage structure were mainly related to changes in abundance of syngnathids and labrids, with the small syngnathid, *Syngnathus abaster*, more abundant in a more elevated intertidal area of the marsh, while larger syngnathids such as *Nerophis ophidion* and *Syngnathus typhle*, and the labrid *Symphodus cinereus*, are more abundant in the subtidal areas. Malavasi et al. (2007) reported a certain degree of habitat segregation between these 3 syngnathids in a Mediterranean coastal lagoon, probably related with a combination of several factors, such as structural complexity, predation, and competition.

Within the unvegetated habitat there were significant differences between sites in terms of fish abundance, fish diversity, and assemblage structure. Differences in fish diversity, although not tested, were negatively related to site elevation, where sites located in more elevated locations within the marsh (sites A and B), and consequently further way from subtidal areas, presented a lower diversity than the site located closer to the subtidal edge (site C). Similar results were reported by Thomas & Connolly (2001) in Western Australia, with fish diversity decreasing with distance from the marsh. In addition to site elevation, it was possible to positively relate fish abundance with the amount of marsh area drained through each unvegetated creek, since fish abundance was higher, in particular for *Pomatoschistus microps* and *Atherina presbyter*, in sites that drained larger saltmarsh areas. This supports the idea that these species follow the tide edge, becoming trapped within the marsh area and concentrated in very shallow intertidal pools formed along tidal creeks at low tide (Crabtree & Dean 1982, Kneib 1997).

Seasonal differences and nursery value

Annual fluctuations in the presence and abundance of YOY from MM and LR were responsible for comparable seasonal changes in fish assemblage structure in both habitats. The abundant presence of YOY in the spring, in particular of MM species, represented a clear seasonal discontinuity in the structures of the fish assemblages of the 2 habitats. During the summer and autumn, YOY abundance progressively decreases, becoming almost absent in winter.

This seasonal pattern is related with the recruitment of early life history stages of MM species, which enter the lagoon in late winter and spring, with most returning to the adjacent coastal waters as juveniles or maturing adults in late autumn and winter (Monteiro et al. 1987, Erzini et al. 2002, Ribeiro et al. 2006). The recruitment of MM species during the spring and summer is consistent with the late winter and spring spawning season of most of these species (Gonçalves & Erzini 2000a,b). The decline in numbers in autumn and winter, both in intertidal and subtidal areas is associated with migrations out of the lagoon to the adjacent coastal waters (Monteiro et al. 1987, Erzini et al. 2002, Ribeiro et al. 2006).

Seasonal fluctuations in the dominant LR species were also responsible for changes in fish assemblages, in particular in the unvegetated habitat, where *Pomatoschistus microps* abundance is higher in the summer and lower in spring, superimposing lower and higher diversity index values in summer and spring, respectively. *Atherina presbyter* was also abundant in the unvegetated habitat from summer to autumn, when the recruits settle in the intertidal marsh area. In contrast, the syngnths, the most abundant group of resident species present in vegetated habitats, are more abundant in the autumn and winter when the YOY recruit after the reproduction season during spring and summer.

Both seagrass and unvegetated shallow habitats within the Ria Formosa intertidal saltmarsh creeks sustain significant populations of juvenile fish of LR and MM species, some of them commercially important. A number of studies carried out in different parts of the world showed that these 2 habitats are important nursery habitats (Cain & Dean 1976, Weinstein 1979, Bozeman & Dean 1980, Weinstein et al. 1980, Rountree & Able 1992). The contrasting fish community structure within the 2 habitats indicates that each provides a distinctive nursery area for different fish species. Unvegetated intertidal creeks were an important habitat for early life stages from LR species *Atherina presbyter*, and for MM species such as *Chelon labrosus*, *Dicentrarchus labrax*, and *Liza aurata*, while seagrass has a similar role for small labrids and plays an important role in the settlement of juvenile syngnths. The average length for most important MM species and for the LR species *A. presbyter* was significantly different in both habitats. In the unvegetated habitat only very early juvenile stages were present, while more advanced juvenile stages were dominant in the seagrass, suggesting an ontogenetic change in habitat for these species.

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